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AVIAN PREDATION INTENSITY AS A DRIVER OF CLINAL VARIATION IN COLOUR MORPH FREQUENCY

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SUMMARY

1) Phenotypic variation provides the framework for natural selection to work upon, enabling adaptive evolution. One of the most discernible manifestations of phenotypic variability is colour variation. When this variation is discrete, genetically-based colour pattern morphs occur simultaneously within a population.

2) Why and how colour polymorphisms are maintained is an evolutionary puzzle. Several evolutionary drivers have been hypothesized as influencing clinal patterns of morph frequency, with spatial variation in climate and predation being considered especially important. Despite this, no study has examined both of their roles simultaneously. The aims of this study were to: 1) examine the covariation of physiology, environmental variables, and colouration at a local scale; and 2) determine if these factors and their interplay explain broad clinal variation in morph frequency.

3) We used the lizard *Liopholis whitii* as a model system, as this species displays a discrete, heritable polymorphism for colour pattern (plain-backed, patterned morphs) whose morph frequency varies latitudinally. We measured reflectance, field activity

temperatures, and microhabitat structure to test for differences in crypsis, thermal biology, and microhabitat selection of patterned and plain-backed morphs within a single population where colour morphs occur sympatrically. We then used data from the literature to perform a broad-scale analysis to identify whether these factors also explained the latitudinal variation of morph frequency in this species.

4) At the local scale, plain-backed morphs were found to be less cryptic than patterned morphs while no other differences were detected in terms of thermal biology, dorsal reflectance, and microhabitat use. At a broader scale, predation was the most influential factor mediating morph frequency across latitudes. However, the observed pattern of morph frequency is opposite to what the modelling results suggest in that the incidence of the least cryptic morph is highest where predation pressure is most severe. Clinal variation in the level of background matching between morphs or the potential reproductive advantage by the plain-backed morph may, instead, be driving the observed morph frequency.

5) Together, these results provide key insights into the evolution of local adaptation as well as the ecological forces involved in driving the dynamics of colour polymorphism.

KEYWORDS

climate, latitudinal cline, evolution, local adaptation, phenotypic variation, reflectance, spectrometry, thermal biology

INTRODUCTION

Across the animal kingdom, phenotypic variation provides the framework for natural selection to work upon, and consequently the process of adaptive evolution. Such variation can be expressed in the form of behavioural (Dall, Houston & McNamara 2004), physiological (Speakman, Król & Johnson 2004) or morphological differences (Endler 1995). One of the most discernible manifestations of phenotypic variability is colour. Not only does colour vary between species, but individuals within a single species can demonstrate striking variation in their colouration as well. When discrete, genetically-based colour pattern variants, or morphs, occur simultaneously within a population the species is referred to as polymorphic (Ford 1945; Huxley 1955; Forsman & Shine 1995a; Ajuria Ibarra & Reader 2013). Colour pattern polymorphism is widespread in nature, evolving repeatedly across taxa. Examples range from invertebrates (Ford 1945; Ahnesjö & Forsman 2006; Davis *et al.* 2008), to mammals (Hoekstra, Drumm & Nachman 2004), birds (Galeotti *et al.* 2003; Roulin 2004), fish (Hancox, Wilson & White 2012; Kraft *et al.* 2016), amphibians (Highton 1959; Hoffman 2000; Wente & Phillips 2003; Hantak & Kuchta 2017), and reptiles (Forsman & Shine 1995a; Stuart-Fox *et al.* 2004; Chapple *et al.* 2008; Broennimann *et al.* 2014; Geen & Johnston 2014b; Pérez i de Lanuza & Font 2015).

Why and how colour polymorphism is maintained has long presented itself as an evolutionary puzzle (Moment 1962; Jones *et al*. 1977; Ajuria Ibarra & Reader 2013). It is well established that colour contributes directly to an individual's fitness in terms of its performance and survivorship (Forsman *et al.* 2008; Ajuria Ibarra & Reader 2013). Under any given ecological circumstance each morph incurs differential costs and benefits (Cain & Sheppard 1954; Watt 1968; Jones, Leith & Rawlings 1977). Where fitness does vary among morphs, selection should eliminate those with lower fitness (Slatkin 1978; Wellenreuther,

Svensson & Hansson 2014). Yet the coexistence of variant morphs still persist within and between populations, albeit at different frequencies.

Several evolutionary drivers have been hypothesized to influence spatial variation in the presence and frequency of colour morphs, including sexual selection, fitness trade-offs, frequency-dependent selection, and genetic drift (Gray & McKinnon 2007; Pérez i de Lanuza, Carretero & Font 2017). Alternatively, shifts in selection pressures associated with macro- and micro-geographic variation in biotic and abiotic factors may instead cause this spatial divergence in colour morph composition to emerge (McLean, Stuart-Fox & Moussalli 2015). One selective force considered to be of prime importance is predation (Endler 1978; Stuart-Fox *et al.* 2004; Schaefer & Stobbe 2006). Body colouration plays a critical role in the evasion of visually-oriented predators as it can serve as a warning (i.e., aposematism) or, by contrast, can impair detection by reducing the contrast between an animal and its background (i.e., crypsis through background matching) (Endler 1984; Stevens & Merilaita 2009). The ultimate efficacy of cryptic colouration is therefore highly dependent upon the visual properties of the animal colour pattern as perceived by the predator relative to the properties of the habitat (Endler 1978). Different morphs, according to theory, should therefore evolve in environments which minimize contrast between its colour pattern and its background, thereby conferring the greatest level of fitness (Ahnesjö & Forsman 2006; Kiernsmo & Merilaita 2012; Marshall, Philpot & Stevens 2016).

Given that the majority of animals occur in visually patchy habitats, varying continuously in colour and texture, there is a strong trade-off between matching some backgrounds at the expense of others (Michalis *et al*. 2017). It can be expected then that the proportion of each morph in a population could be a function of its ability to adequately match the available

backgrounds in order to minimize detection from potential predators (Cain & Sheppard 1954; Cain & Currey 1963; Endler 1978; Gardner *et al.* 1995; Chapple *et al.* 2008). In other words, each morph would occur more frequently within habitats which are dominated by backgrounds which promote crypsis for their particular colour patterning. While the alternate morph would be more conspicuous, resulting in potentially greater levels of predation, reducing their frequency. Indeed, the strong effects of background matching on predation rates among polymorphic species by visual hunters has been empirically demonstrated (Gibbons & Lillywhite 1981; Forsman & Shine 1995a; Wente & Phillips 2003; Stuart-Fox *et al.* 2004; Hoekstra 2006).

Alternatively, the occurrence and maintenance of colour polymorphism may instead be promoted by negative frequency dependent selection where the common morph is disproportionately predated upon than the others (Endler 1988). This results in the rare morph becoming advantageous against the common morph, regardless of level of crypsis exhibited among morphs (Punzalan *et al*. 2005). Search image formation has generally been evoked as the mechanism underlying the variation in the level of focus by predators for a particular morph, but its existence is controversial (Endler 1988). Moreover, direct evidence of frequency dependent selection is limited (although see Bond & Kamil 1998; Fitzpatrick, Shook, & Izally 2009; Olender et al. 2016) due to the challenge of testing the theory under natural conditions.

In addition to predation, the interplay between thermal physiology and climate is also thought to be a major adaptive force driving spatial variation of colour polymorphic species (Roulin 2004; Rosenblum & Beaupre 2005; Ahnesjö & Forsman 2006; Alho *et al.* 2010; Broennimann *et al.* 2014; McLean & Stuart- Fox 2014; McLean *et al*. 2015). Colouration

interacts with incoming solar radiation, which causes heat energy to either be absorbed into the body or reflected away, influencing an individual's thermoregulatory efficiency (Galeotti *et al.* 2003; Clusella-Trullas *et al.* 2008; Harris, McQuillan & Hughes 2012; Galván, Palacios& Negro 2017). Darker coloured morphs, in having lower reflectance, tend to absorb more incident radiant energy resulting in faster heating rates and higher equilibrium temperatures (Stoner *et al*. 2003; Roulin 2004; Rosenblum & Beaupre 2005; Broennimann *et al.* 2014). Greater and more rapid heat gain promotes optimal physiological function and performance (Ahnesjö & Forsman 2006; Geen & Johnston 2014a). Thus, dark colouration confers a thermal advantage under low climatic and/or ambient light conditions through the lengthening of activity periods as well as increased growth rate and reproductive output (Broennimann *et al.* 2014). Lighter coloured morphs, on the other hand, are apparently better adapted to hotter climatic and higher light conditions as their colouration acts to reflect a greater amount of radiant energy. This slows heating rates and lowers equilibrium temperatures, thereby minimizing the risk of exceeding critical thermal limits in hot environments (Tattersall, Eterovick, & de Andrade 2006). Such variation in morph frequency as a function of temperature and/or light conditions has also been well documented (Forsman & Shine 1995a; Parkash, Rajpurohit & Ramniwas 2008; Alho *et al.* 2010; Broennimann *et al.* 2014; Geen & Johnston 2014a; McLean, Stuart-Fox & Moussalli 2015). Furthermore, several other studies investigating the effect of skin reflectance on thermal traits, such as heating rates and equilibrium temperatures, have also shown strong support for the thermal advantage of colour (Schultz & Hadley 1987; Forsman 1995a; Forsman *et al.* 2002; Tanaka 2007; Alho *et al.* 2010; Geen & Johnston 2014a; Sanabria *et al.* 2014). For instance, in a large-scale macroecological study involving 66 species of heliothermic lizards, Clusella-Trullas *et al.* (2008) found that skin reflectance was positively related to mean annual temperature as well as global solar radiation. In other words, in cooler climates lizards tended to absorb more

radiant energy whereas in warmer climates more solar radiation was reflected away from the body.

Precipitation, too, is another climatic variable that has been shown to dictate the spatial patterns of polymorphic species (Lai *et al*. 2007; Harris *et al*. 2012; Broennimann *et al*. 2014; McLean *et al*. 2015). Higher levels of rainfall tend to be associated with darker coloured individuals both among ectotherms as well as endotherms. This is demonstrated in such species as the wingless grasshopper (*Phaulacridium vittatum*) (Harris *et al*. 2012), adder (*Vipera berus*) (Broennimann *et al*. 2014), asp viper (*V. aspis*) (Broennimann *et al*. 2014), and house mice (*Mus musculus*) (Lai *et al*. 2007). But despite this extensive evidence for the importance of climate, particularly temperature, in driving spatial variation in morph frequency, there are still some studies which do not support these hypotheses (Crisp, Cook & Hereward 1979; Bittner *et al.* 2002; Umbers, Herberstein & Madin 2013). Among these, the interaction between solar radiation and dermal colouration had no effect on heating rates or equilibrium temperatures and thus colour did not confer a thermal advantage.

Given that functional trade-offs between predator avoidance and thermal physiology may exist, it is less clear as to which is more influential or what their combined effect may be on colour polymorphism. Disentangling the relative influence of these factors has yet to be explored. Fortunately, polymorphic species commonly exhibit a phenomenon of ratio clines which may prove invaluable to our understanding of the mechanisms underlying colour polymorphism (Galeotti *et al.* 2003). Ratio-clines are graded alternations of morph frequency across ecological gradients. Much evidence exists indicating that ratio-clines arise as a result of broad-scale spatial variation in selective pressures, such as climate and predation (Wise & Reillo 1985; Hoekstra *et al*. 2004; Phifer- Rixey *et al.* 2008; Broennimann *et al*. 2014; McLean and Stuart-Fox 2014). For example, in a phylogenetic analysis conducted by Galeotti *et al*. (2003), study results suggested that geographic patterns of morph frequency likely

evolved as a function of predator detectability. Dark morphs occurred more frequently in the cloudy and wet climates of high latitudes as they were more cryptic under such conditions relative to paler morphs. Similarly, albeit at a finer geographic scale, the frequency of light and dark coloured morphs of flat periwinkles (*Littorina obtusa*) varied between populations within a coastal intertidal zone (Phifer- Rixey *et al.* 2008). Dark morphs occurred more readily under colder conditions while the light-shelled variants were more prevalent in sites with warmer conditions.

Here, we aimed to evaluate the interactive effects of environment and predation in order to identify the ecological forces that explain the occurrence of colour polymorphism. Specifically, we wanted to test the competing hypotheses that either crypsis or thermoregulation maintain geographic variation in morph frequency using the lizard *Liopholis whitii* (White's skink) as a model system. This species displays a discrete, heritable polymorphism for colour pattern whose morph frequency varies latitudinally (Chapple *et al*. 2008) (Fig. 1). We began by first conducting a field study at a local scale to test for differences in microhabitat selection, thermal biology, and crypsis between morphs within a single population where plain-backed and patterned morphs occur sympatrically. As selective agents may operate differentially between males and females, sexual variation within morphs was also assessed. Broad scale analyses were then performed by collecting morph frequency data across this species' latitudinal distribution and comparing these data with local climate and predation risk in order to identify the primary factor(s) involved in explaining clinal variation in morph frequency. If climate were the driving force, it would be expected that morphs having lower reflectance would have a higher frequency in cooler climates as darker colouration should increase heating rates and thus confer a thermal advantage. Conversely, if polymorphism was more influenced by predator avoidance by way of crypsis, then we would

expect morph frequency to vary according to predation pressure. Under this premise, the least conspicuous morph with the lowest contrast to its background would have a higher overall occurrence rate as well as greatest frequency in latitudes with the most visually-orientated predators.

METHODS AND MATERIALS

Study species and field collection

Liopholis whitii (snout-vent length [SVL] 51-113 mm) is a diurnal, rock-dwelling heliotherm whose geographic distribution spans along eastern Australia from south-eastern Queensland through to northern Tasmania (Fig. 1) (Donnellan *et al.* 2002). Primary habitat associations include eucalypt dominated open-forests, sandy coastal areas, woodlands, tussock grasslands and open heathlands (Chapple 2003). Its main predators are birds, snakes, and mammals (Chapple 2003).

Liopholis whitii exhibits three discrete colour morphs that are not related to sex and do not change with temperature, as seen in other species. The three morphs include: a) a patterned morph whose dorsal and lateral patterning appears visually darker in colouration (Fig. 1a); b) a plain-backed morph lacking dorsal patterning and visually lighter in colour (Fig. 1b); and c) a patternless morph which lacks both dorsal and lateral patterning. This polymorphic colouration is heritable following Mendelian inheritance (Milton 1990; Chapple *et al.* 2008). The relative frequency of each morph varies latitudinally across its range (Fig. 1) (Chapple *et al.* 2008). The patterned and plain-backed morphs are the two more common forms and are sympatric throughout most of the species' range. They show opposing patterns of variation where the patterned morph increases with latitude while the plain-backed morph generally decreases with latitude. The patternless morph, on the other hand, is restricted to a narrow

band (34–38°S) revealing no latitudinal pattern (Chapple *et al.* 2008) and is thus not included in this study. Few subtle differences in habitat preferences and fecundity have been observed among the three colour morphs, although morphologically, they have not been found to vary other than in colouration (Milton & Hughes 1986; Milton 1990; Chapple 2003; Chapple & Keogh 2004; Chapple 2005; Chapple *et al.* 2008). For instance, Milton (1990) found some evidence that plain morphs prefer more rocky microhabitats than patterned morphs. And Chapple (2005) showed that plain-backed females produced larger litters. However, no studies have directly investigated physiology or crypsis nor have any addressed how these potential differences might relate to the maintenance of colour polymorphism.

The field study was conducted in October and November of 2015 in a single *L. whitii* population comprised of both patterned and plain-backed individuals. The site is a 20,500-ha patch of continuous dry-wet sclerophyll forest (Watson and Wardell-Johnson 2004) that spans the border between Girraween National Park (QLD) and Bald Rock National Park (NSW). Lizards were caught along two adjacent 1-km transects flanking Bald Rock Creek in Girraween National Park, and at a single location in Bald Rock National Park (28.86064° S, 152.03397° E) during their normal activity period (8:00-17:00). Lizards were located by visually scanning while walking a transect, or by actively lifting small rocks and then captured either by hand or noose. Upon capture, individuals were assigned their appropriate colour morph, sexed, tail condition assessed (full, partial, or regenerated), thermoregulatory activity (basking position or in a shelter) recorded, and the following measurements taken: cloacal body temperatures (field body temperature = T_b) using a T-type thermocouple and digital thermometer (Eutech Instruments model PT100), surface temperature of capture site (selected environmental temperature = T_e), and air temperature (T_a) 2-4 cm above capture site. And as morphological characters can also evolve in concert with colouration (Ahnesjö &

Forsman 2006), weight (± 0.01 g), snout vent length (SVL), tail length (TL), body width (BW), head length (HL), head width (HW), forelimb length (FLL), hindlimb length (HLL) and interlimb length (ILL) were also recorded.

Thermal biology

Measurement of heating rate

Heating rate was measured either in the field or at the field station when ambient temperatures were too high for equipment to operate. Procedures were identical under both experimental conditions. Tests were performed using an aluminium-lined thermal chamber (9 cm^3) and acclimation chamber (30 x 20 cm) fitted with a glass lid and powered by a 12 V lithium ion battery. Prior to the test, lizards were placed in the acclimation chamber set to 20 °C for 10 min in order to get all lizards to the same starting body temperature. Lizards were then transferred to the thermal chamber set to 35 °C. Dorsal body temperatures were recorded every minute for 10 min using a Fluke 566 IR thermometer gun (Fluke Australia). Tests were concluded once the lizard's body temperature reached 35 °C (approximately this species' preferred body temperature) (Johnson 1977). Body temperature measurements and the time taken to achieve test temperature were used for heating curve analyses.

Effects of dermal reflectance on thermoregulation

As the level of dermal reflectance is thought to influence heat balance, reflectance of lizards on the dorsal and lateral body regions was measured. Prior to measuring, lizards were acclimated to a body temperature of 20 °C in the acclimation chamber. Reflectance was measured between 260 to 700 nm (UV spectrum) spectral ranges using an AvaSpec 2048 spectrometer and a pulsed xenon light source (AvaLight-Xe, Avantes, The Netherlands) connected through a bifurcated fibre-optic probe. The probe was fitted at the tip with a plastic

cylinder to standardise measuring distance and shield out ambient light and placed perpendicularly to the body on the following six positions: upper and lower dorsal regions, upper and lower right lateral regions, as well as the upper and lower left lateral regions (Fig. S1) resulting in a total of six measurements per lizard. Reflectance of each position was calculated relative to a WS-2 white standard. Raw spectra data were obtained with the program AvaSoft 7.5 and smoothed using a running average computed over a 20-nm interval. Average dorsal and lateral reflectance of individual lizards was used to assess variation among morphs and also served as input data in the analyses modelling background matching.

Microhabitat characterization and background matching

Microhabitat was assessed by centring a 50 cm^2 quadrat over the position at which each lizard was first observed. Within the quadrat, percent vegetation cover was measured at <1 m, 1-2 m and >2 m in height and one of three microhabitat types assigned: open rock, leaf litter or vegetated. Open rock was defined as sites having little or no vegetation present and substrate consisting predominantly of uncovered rock. Leaf litter was defined as sites predominantly covered with a layer of leaf litter. Vegetated sites were defined as having at least 60% of the substrate shaded by vegetation less than 2 m in height.

Background reflectance was quantified in order to evaluate variation in the level of background matching between morphs. Major colour groups of the substrate were identified and their approximate percentage within each quadrat was recorded (Fig. S2). Colour groups included: light granite, dark granite, light rock, dark rock, grey leaf litter, red leaf litter, green vegetation, dirt, stick, green moss, blue moss, orange moss, and yellow moss. Reflectance of the substrate was then measured by placing the spectrometer probe on a single position of each colour group following the methods previously described (see *Effects of dermal*

reflectance on thermoregulation) to produce a single reflectance value for each colour group within the quadrat. For those quadrats containing slight variations within a major colour group, multiple measurements were taken and the reflectance values averaged.

Statistical analyses

All data were tested for normality and non-parametric tests were used for those data not meeting normality. Morphological measures (mass and FLL), microhabitat percentage cover, achromatic variation could not be transformed thus non-parametric test were instead performed. Statistical significance was established at $\alpha = 0.05$. Analyses on morphology were restricted to adults (SVL > 80 mm; Milton, 1987) whereas analyses on thermal biology, microhabitat use, and background matching included both adults and juveniles.

Morphology

General linear model ANOVAs were constructed to test for differences between sexes and morphs in morphology, including SVL, mass, HL, HW, HLL, IIL, BW and TL (n = 45, patterned morph = 18, plain-backed morph = 27; SPSS v. 23, IBM). Sex, morph, and their interaction were fixed factors and SVL was a covariate. Tail length was compared only for adults with original tails (n = 32, patterned morph = 17, plain-backed morph = 15). Comparison of tail loss frequency was tested using a generalized linear model (GLM) with a binomial error distribution and 'probit' link function (n =64, patterned morph = 31, plain-backed morph = 33). Tail loss (binary: 'yes' or 'no') was modelled as a function of morph, sex, as well as their interactions.

Thermal biology

Comparison of thermoregulatory behaviour was tested using a GLM with a binomial error distribution and 'probit' link function (*n* = 64, patterned morph = 31, plain-backed morph = 33). Basking (binary: 'yes' or 'no') was modelled as a function of morph, sex, as well as their interactions. Field body temperature (cloacal temperature) and selected environmental temperature (substrate temperature) were analysed using general linear model ANOVAs (*n* = 58, patterned morph = 27, plain-backed morph = 31: SPSS v. 23, IBM). Morph and sex as well as their interactions were included as fixed effects and SVL was a covariate. To compare heating rate between morphs and sexes, a thermal time constant value was calculated for each heating rate curve (Dzialowski & O'Connor 2001). The thermal time constant (τ) was calculated by taking the inverse of the slope of a linear regression of $\ln(T_b - T_a)$ against time (Bressin & Willmer 2000; Rice, Roberts & Dorcas 2006; Zhang *et al.* 2008). As several *L. whitii* individuals surpassed 35 °C (T_a) within their test period, only data which had at least seven consecutive time points that fit the criteria of the regression model were included (*n* = 39). Tests of linearity for each regression model was used to identify heating rate curves which were not exponential with those failing the test being excluded from the analyses. The influence of sex and morph on heating rate was assessed using a GLM (*n* = 28: patterned morph = 13, plain-backed morph = 15; SPSS v. 23, IBM). Thermal time constant was the response variable whereas morph, sex, and their interaction were used as fixed effects and SVL was included as a covariate. GLMs were also used to model the influence of morph and sex on reflectance. Response variables included average dorsal reflectance as well as left and right lateral reflectance. Morph, sex, and their interaction were used as fixed effects and SVL was included as a covariate (SPSS v. 23, IBM).

Microhabitat selection and background matching

Variation in the types of microhabitat used between morphs and sexes was assessed using a Fisher's exact test (*n* = 64, patterned morph = 31, plain-backed morph = 33; SPSS v. 23, IBM). Spearman's rho was used to test for correlations between vegetation cover at < 1 m, 1-

2 m, and > 2 m within selected microhabitats. No correlations were found thus all variables tested (% cover < 1 m and % cover 1-2 m: $r = 0.10$, $P = 0.42$; % cover < m and % cover > 2 m: $r = -0.12$, $P = 0.36$; % cover 1-2 m and % cover 1-2 m: $r = 0.17$, $P = 0.17$). GLMs were used to evaluate the effects of morph type on microhabitat selection (SPSS v. 23, IBM). A Tweedie distribution (due to the large number of zeroes) with a "log link" function was used with Pearson chi square as the scaling factor. Microhabitat type and percent cover were response variables and morph, sex, and their interactions were fixed effects and SVL was included as a covariate. Background reflectance was determined by calculating the sum of the weighted average reflectance for each colour group within individual microhabitats. Differences in colour group reflectance values between selected microhabitats was evaluated using ANOVA (SPSS v. 23, IBM). Variation in background reflectance of selected microhabitats between morphs and sexes was analysed using general linear model ANOVAs. Morph and sex and their interactions were included as fixed effects and SVL was a covariate.

Background matching was evaluated by calculating chromatic (colour) and achromatic (light to dark) contrasts between the dorsal reflectance of individual lizards against their backgrounds using psychophysical models of avian colour vision. Visual modelling was performed in R computing environment (version 0.99.893) using R functions as described in Delhey *et al.* (2015) which implement receptor-noise-limited visual models (Vorobyev & Osorio 1998) following Cassey *et al.* (2008). Colour vision in birds is mediated by four types of single cone sensitivities, those that are sensitive to very short, short, medium and long wavelengths of light (VS, S, M and L respectively). Birds typically have one of two types of cone sensitivity functions (more and less UV-sensitive, U-type and V-type, respectively (Endler & Mielke 2005) and species belonging to both types are present across avian skink predators (Ödeen *et al*. 2011; Ödeen & Håstad, 2013). We used average V-type and U-type

cone sensitivities for the analyses obtained from Endler and Mielke (2005). But given that U and V-type visual sensitivities do not differ in terms of double cone sensitivity function, achromatic contrasts were only analysed using U-type. In addition to cone sensitivity functions, visual models require knowledge on the noise-to-signal ratios of each photoreceptor and the spectrum of the light source that provides illumination (Vorobyev *et al.* 1998). Noise-to-signal ratios for each single cone were obtained using formula 10 in Vorobyev *et al.* (1998), a Weber fraction of 0.1 for the L cone (Lind, Chavez & Kelber 2014; Olsson *et al*. 2018) in combination with the relative abundance of each cone type in the avian retina. Average cone proportions (0.38:0.69:1.13:1, VS:S:M:L respectively) were obtained from (Hart 2001). Finally, we ran models using the standard daylight spectrum (D65) as well as woodland shade as the illuminant to account as lizards were captured primarily within open sunny areas and woodland habitats (Vorobyev *et al.* 1998).

Using the described approach, cone quantum catches, or the degree to which spectra stimulate each single cone type are converted into a set of three XYZ chromatic coordinates that define the position of each reflectance spectrum in the visual space of birds (Delhey *et al.* 2015). Using the formulas from Cassey et al. (2008) distances between points in visual space are measured in JNDs (just noticeable differences) whereby, in general, values below 1 JND are thought not to be discriminable, while values above this threshold become progressively easier to discriminate. However, this value should not be taken as a categorical threshold given the uncertainties in the parameters used to compute contrast values (Kemp *et al.* 2015), due to the fact that this information is not available for most avian predators and we are extrapolating based on data from other species. Thus, Euclidean distances between XYZ coordinates of lizards and those of their natural backgrounds provide the level of chromatic contrast.

Visual models, as outlined above only take into consideration the chromatic channel, discarding achromatic variation. Achromatic variation in birds is presumed to be mediated by double cones and hence for each reflectance spectrum we also computed the double cone quantum catch. The level of achromatic contrast between each lizard and its habitat was computed using formula 7 in Siddiqi *et al.* (2004) assuming a Weber fraction of 0.2 (Olsson, Lind and Kelber 2018). And like chromatic contrasts, achromatic contrasts are also measured in JNDs.

For each lizard, we computed an average value of contrast between each dorsal reflectance measure (upper, lower, and average dorsal) and its background. Chromatic and achromatic contrasts were analysed separately for each of the different visual cone sensitivity functions and illuminants. This was done by first computing chromatic and achromatic contrasts between the lizard and each colour group found within the quadrat. The percent cover estimates for each colour group was then used to obtain a weighted average contrast for each lizard. Hence, colours that had high percent cover within the quadrat contributed more to the weighted average contrast. These weighted contrasts served to estimate the extent to which lizards matched their backgrounds in terms of chromatic and achromatic cues. Note that we did not measure pattern matching as this requires a quantification of the spatial distribution of the different colours in the background (e.g., (Troscianko *et al*. 2016).

General linear model ANOVAs were used to model the influence of morph and sex on chromatic contrasts while GLMs were used for achromatic contrasts (n = 65, patterned morph = 31, plain-backed morph = 34; SPSS v. 23, IBM). Response variables for each of the models

were upper, lower, and average dorsal contrasts. Morph and sex were used as fixed effects and SVL was included as a covariate.

Modelling latitudinal drivers of morph frequency

A model comprised of morph frequency, climatic variables, and predation pressure was used to determine the factors influencing latitudinal variation in morph frequency observed in *L. whitii* (SPSS v. 23, IBM). To do this, morph frequency, predation pressure, and climatic conditions were assessed within each of eight discrete latitudinal bands spanning the geographic range of this species (Band 1: 26-28 °S, Band 2: 28-30 °S, Band 3: 30-32 °S, Band 4: 32-34 °S, Band 5: 34-36 °S, Band 6: 36-38 °S, Band 7: 38-40 °S, Band 8: 40-44 °S) (Chapple *et al.* 2008). The number of patterned and plain-backed individuals were estimated in each band using museum specimens from all major Australian museums including the Australian Museum, Queensland Museum, CSIRO Australian Wildlife Collection, Museum Victoria, Tasmanian Museum and Art Gallery (TMAG), Queen Victoria Museum (QVM), South Australian Museum (SAM), Western Australian Museum (Goswami *et al.*), and the Northern Territory Museum and Art Gallery (NTMAG) (Table S1). Climatic variables were selected based on their interactive effects on dermal colour and thermoregulation and included average annual rainfall and average annual maximum and minimum temperature (Climate Data Online, Bureau of Meteorology). Each climatic variable was averaged across available years for each latitudinal band. Measuring predation pressure directly is inherently difficult thus quantifying predator diversity is often used as a proxy (Morlon, Kefi, & Martinez 2014; Valcu *et al*. 2014; López-Villalta 2016; Kotrschal *et al*. 2017). Accordingly, predation pressure was quantified using presence-absence data on all mammal, reptile, and avian species known to consume skinks (Marchant & Higgins 1990; Higgins & Davies 1996; Davis JR 2001b; Davis JR 2001a; Cogger 2014) (Table S2). From this published data, the

level of predation risk was scored based on the proportion of each species' diet which was made up of skinks. A score of one indicated low level of predation risk (skinks < 10% of diet); two indicated a moderate level (skinks 10-50% of diet), and three was indicative of a high level (skinks > 50% of diet). Scores of all predator group (birds, mammals, and reptiles) were then added together within each latitudinal band. A series of binomial generalised linear models were constructed to determine the level of influence predation and climate had on morph frequency. Avian, mammal and reptile predation pressure, rainfall, minimum and maximum temperature were included as fixed effects and *L. whitii* morph incidence was the response variable, where each occurrence of a patterned skink was considered a success and each occurrence of a plain skink a failure (e.g. binary: patterned = 1; plain-backed = 0). Using the 'PerformanceAnalytics' package in R (Peterson *et al*. 2014), all explanatory variables were tested for correlation. The models did not include interactions between avian, reptile and mammal predators as they were significantly correlated with an absolute correlation coefficient greater than 0.8 (bird-reptile R = 0.92; bird-mammal R = -0.98; mammal-reptile R = -0.84). Thus, only interaction terms between rainfall, maximum temperature, and a single predator category was included. The package 'bbmle' in R (Bolker 2011) was used to compare the AIC of each model. Final model selection was assessed using the Akaike's information criterion (AIC). Models having AIC scores differing from that of the lowest score by less than two (i.e. ΔAIC < 2) would also be considered as supported (Dochtermann & Jenkins 2007).

RESULTS

Morphology

A total of 34 plain-backed (males = 20; females = 14) and 31 patterned (males = 17; females = 14) *L. whitii* individuals were captured. Of these, 27 were adult plain-backed (males = 16;

females = 11) and 19 were adult patterned (males = 12; females = 7) individuals with the remaining being juveniles (Table 1). No morphological traits aside from colouration varied between morphs (Table 2). However, males had longer heads than females, and variation in interlimb length was affected by the interaction between morph and sex. Females had longer interlimb length than males with plain-backed females having the longest trunks. The incidence of tail loss was not different between morphs ($\chi^2 = 0.47$, df = 1, $P = 0.49$) but was influenced by sex ($\chi^2 = 40.10$, df = 1, $P < 0.01$) and its interaction with age ($\chi^2 = 58.86$, df = 1, $P < 0.01$) where juvenile females were found to have the greatest frequency of tail autotomy.

Thermal biology

Thermoregulatory behaviour was not influenced by morph, sex, or their interaction ($F = 0.70$, df = 1, $P = 0.24$; $F = 2.51$, df = 1, $P = 0.11$; $F = 0.74$, df = 1, $P = 0.39$, respectively; Table 3). Morph did not correlate with either field body temperature or selected environmental temperature ($F = 8.10$, df = 1, $P = 0.99$; $F = 0.65$, df = 1, $P = 0.42$, respectively; Table 3). The effect of sex on field and environmental temperatures approached significance ($F = 3.45$, df = 1, $P = 0.07$), with females having slighter higher body temperatures ($\mu = 31.83$ °C, SE = ± 0.35) than males ($\mu = 30.03$ °C, SE = ± 0.42). Similarly, neither morph, sex, or their interaction had an effect on heating rates ($F = 0.19$, df = 1, $P = 0.67$; $F = 0.02$, df = 1, $P = 0.90$; $F = 0.16$, df = 1, $P = 0.70$, respectively; Table 3).

Average dorsal reflectance was higher among patterned morphs (6.98 to 25.80 nm; $\mu = 14.46$ nm, SE = ± 4.99) than plain-backed morphs (7.92 to 20.83 nm; $\mu = 13.80$ nm, SE = ± 3.75). Similarly, average reflectance of the lateral regions of patterned morphs was again higher than that of plain-backed morphs. Left and right lateral positions ranged from 8.82 - 37.15 nm

(μ = 22.37 nm, SE = ± 6.56) and 11.53 – 42.93 (μ = 22.57 nm, SE = ± 7.16), respectively for patterned morphs. Whereas plain-backed morphs had ranges of 8.32 – 40.59 nm (μ = 20.37 nm, SE = ± 6.85) for the left lateral side and 10.56 – 33.58 nm (μ = 21.77 nm, SE = ± 5.51) for the right side. Variation between morphs in average dorsal and lateral reflectance was not detected (Table 3). However, right lateral differed with sex (χ^2 = 5.02, df = 1, P = 0.03), whereby females had higher reflectance than males.

Microhabitat selection

Selection of microhabitat type did not differ between morphs (χ^2 = 1.16, df = 2, P = 0.56) or sexes (χ^2 = 0.56, df = 2, P = 0.97; Table 4). However, the use of microhabitat did differ between sexes of each morph (Fig. 2). Plain-backed females preferred open sites with rocky substrate to the highest extent while patterned females tended to select vegetated microhabitats. Among males, both morphs, particularly patterned, selected open rocky sites most often. Microhabitats with leaf litter were used the least among all lizards.

Within individual microhabitats, the amount of vegetation cover at all three heights did not vary according to morph or sex (Table 4). However, there was a significant interaction between these two factors at both the < 1 m (χ^2 = 11.18, df = 1, P < 0.001) and 1-2 m heights (χ^2 = 5.92, df = 1, P = 0.02). Overall, patterned females selected sites with the greatest amount of vegetation cover and plain-backed females selected the least open sites. By contrast, patterned males utilized sites with low vegetation cover and plain-backed males occurred most often in microhabitats with greater levels of cover. No variation in vegetation cover at > 2 m was detected between morphs (χ^2 = 0.67, df = 1, P = 0.41), sexes (χ^2 = 1.23, df = 1, P = 0.27), or their interaction (χ^2 = 1.15, df = 1, P = 0.28).

A total of 381 reflectance measurements were taken of the microhabitat with an average of six measurements per lizard. Colour groups did not vary between selected microhabitats (F = 0.645; df = 64; P = 0.982). Background reflectance within individual microhabitats did not vary between morphs (F = 0.38, df = 1, P = 0.60), sexes (F = 0.83, df = 1, P = 0.36), or their interaction (F = 0.93, df = 1, P = 0.34).

Background matching

The level of chromatic and achromatic contrasts differed slightly according to visual systems and illuminants used in the visual models (Table S3). Chromatic contrasts were lowest for models using the V-type cone sensitivity functions and standard daylight illuminant (2.36 ±0.11) whereas achromatic contrasts were lowest for models using the woodland shade illuminant (2.25 ±0.20). However, the overall patterns of variation among contrasts remained the same.

Average dorsal chromatic and achromatic contrasts of individual lizards to their background (conspicuousness) exceeded the value of 1 for all combinations of model parameters (patterned: mean JND = 2.46 ±0.08; plain-backed: mean JND = 2.80 ±0.08; patterned: mean JND = 2.32 ±0.15; plain-backed: mean JND = 2.19 ±0.13; respectively) suggesting that each morph type is discriminable by avian predators (Fig. 3). The degree to which morphs contrasted their backgrounds varied according to habitat type. Greater levels of background matching occurred for patterned morphs within leaf litter despite the selection of this habitat type being the lowest (n = 3). While plain-backed morphs, on the other hand, were least conspicuous (low contrast) within open rock and vegetated habitats which coincided with high utilization of this habitat type (n = 23, n = 9, respectively; Fig. 3).

Variation in conspicuousness between morphs was detected, however, this was dependent upon the visual system and illuminant used within the models (Table 5). Only models using V-type cone sensitivity functions identified significant differences for achromatic contrasts. Such models indicated that background matching was higher (lower contrast) among patterned morphs of all dorsal regions for the standard daylight illuminant (upper: $F_{1,64}$ = 5.40, P = 0.02; lower: $F_{1,64}$ = 4.66, P = 0.04; average: $F_{1,64}$ = 6.34, P = 0.01; Table 5) where patterned morphs would be discriminated by avian predators less than plain-backed morphs. Conversely, only the upper and average dorsal regions were found to vary between morphs for the woodland shade illuminant (upper: $F_{1,64}$ = 4.71, P = 0.03; lower: $F_{1,64}$ = 3.60, P = 0.06; average: $F_{1,64}$ = 5.24, P = 0.03). Sex was found not to influence chromatic contrasts. In terms of achromatic contrasts, only the upper dorsal region varied between morphs (X^2_1 = 4.19, P = 0.04), with the plain-backed morph having greater background matching abilities. An interaction with morph and sex was also found (X^2_1 = 4.27, P = 0.04), showing that plain-backed males were the least conspicuous whereas the patterned males were the most conspicuous in this body region.

Latitudinal drivers of morph frequency

Our predation risk scores indicated that potential avian and reptilian predation pressure increased with decreasing latitude, whereas the opposite pattern was observed for mammalian predation pressure (Table S2). Of the eight models used to explain the variation in morph frequency across the latitudinal bands, the best model was comprised solely of bird predation whereas the model having only climate performed the worst (Table 6). Model results indicated that the patterned morph, despite being less conspicuous, had a lower probability of occurrence than the plain-backed morph (Z = 8.89, df = 7, P < 0.05) within latitudinal bands having the greatest level of potential avian predation pressure (26-36 °S; Fig. 4). In other words, the patterned morph increased in frequency

with declining predation pressure while the more conspicuous plain-backed morph had increased frequency with increases in predation intensity.

DISCUSSION

Overall, our findings suggest that predation is the key ecological factor which may help explain colour polymorphism in *L. whitii*. At the local scale, only female interlimb length and the level of background matching varied between morphs with the plain-backed morph having longer trunks and being most conspicuous towards avian predators. No other differences were found in terms of thermal biology, microhabitat type selection, or morphological measures, suggesting that predator avoidance could likely be an important functional role of colour in this population. Broad scale analyses paralleled these results in that predation was again identified as the primary ecological force driving latitudinal variation in morph frequency rather than the effect of climate. Paradoxically, modelling results revealed that the incidence of the least cryptic morph (plain-backed) is highest where predation pressure is most severe. Below we discuss potential explanations as to what other mechanisms could be causing these patterns to emerge.

Local adaptation

No variation was detected among thermal traits between patterned and plain-backed morphs, including field active body temperatures, selected environmental temperatures, and heating rates. Individual lizards were instead active at similar body temperatures and within sites having thermal regimes all falling within the same temperature range. The rate of heat absorption was also similar among patterned and plain-backed morphs. These findings coincide with the fact that dorsal reflectance also did not vary between morphs.

The fact that both colour morphs of *L. whitii* do not vary in rate of heat gain, activity and selected environmental temperature, as well as dorsal reflectance suggests that each would respond to the thermal environment in similar ways. Thus, colour does not appear to be affording a thermal advantage within this species. Instead, climatic conditions across habitats would constrain or promote individual thermoregulatory behaviour and surface activity, which would in turn affect foraging, activity periods, reproductive opportunities, habitat use, and ultimately fitness equally, regardless of their colouration. Such results are surprising as they are in stark contrast to our own predictions as well as much of the previous research on polymorphic species (Forsman 1995b; Forsman *et al.* 2002; Clusella-Trullas *et al.* 2008; Parkash, Rajpurohit & Ramniwas 2008; Clusella-Trullas, van Wyk & Spotila 2009; Broennimann *et al.* 2014; McLean, Stuart-Fox & Moussalli 2015). Among these studies, thermoregulatory behaviour and heating rates differed between colour morphs whereby darker coloured individuals who typically inhabited cooler climates gained heat at a faster rate thereby reducing the amount of time engaged in basking behaviour.

However, it should be acknowledged that field constraints and relatively small sample sizes in our study prevented us from measuring heating rates using a radiative heat source which could potentially reveal a difference between morphs in the speed at which heat is gained. Future studies using alternative methodology and larger sample sizes is warranted to better evaluate the thermal biology of this species. But given that our broad-scale results did coincide with our local-scale findings, in that climate was found to be a poor predictor in morph composition of *L. whitii* across its latitudinal distribution, it is possible that there indeed is no thermal advantage conferred by colouration in this species. What's more, similarity in thermal traits and reflectance among morphs is not unheard of and has been

observed. Mojave fringe-toed lizards (*Uma scorparia*), for example, also exhibit comparable solar absorptances between morphs (Norris 1967). As do juvenile garter snakes (*Thamnophis sirtalis*) where melanistic and non-melanistic individuals did not differ in either their heating rates or equilibrium temperatures (Bittner 2002).

The traits which did differ between morphs, however, appear to serve more as a means of predator avoidance than that of a thermoregulatory function. They included microhabitat selection and the level of background matching. For instance, despite similarity in reflectance measures of both lizard dorsal surfaces as well as the selected microhabitats, morphs varied in the level of contrast with their backgrounds. Levels of chromatic contrast for both patterned and plain-backed morphs were relatively low, consistent with their cryptic appearance to human observers. But the plain-back morph was, however, more conspicuous than the patterned morph to avian predators. Although, the lower level of conspicuousness among patterned individuals is contradicted by the lack of variation in the incidence of tail loss between morphs. For this apparent similarity in predation rate to occur, and the plain-backed morph to be maintained, an alternative anti-predatory strategy is likely being employed in order to ameliorate the impacts of having reduced background matching capabilities. Simply utilizing microhabitats which afford greater cover as a means of avoiding detection does not appear to be at play in this population as plain-backed morphs, particularly males, occurred more frequently in open sites than patterned morphs.

Reduced detection of plain-backed morphs by predators may instead be achieved through the use of another form of crypsis, disruptive colouration. Unlike background matching, where interior patterning within the body's edge is background specific, thus requiring low contrast between prey and its surroundings, disruptive colouration serves to camouflage the body

outline (Cott 1940; Stevens 2007; Stevens *et al*. 2009). This interferes with edge detection mechanisms which are vital to a predator's ability to discriminate prey from their background (Karpestam, Merilaita & Forsman 2013). Under this premise, the solid brown dorsal colouration and lateral patterning of the plain-backed morph may serve to enhance camouflage via a disruptive effect (Ahnesjö & Forsman 2006). Because the efficacy of disruptive colouration has been shown to be greater than crypsis, this could explain how the plain-backed morph is able to be maintained within the population despite having a reduced ability to effectively match their backgrounds (Schaefer & Stobbe 2006; Stevens 2007). But whether plain-backed morphs are in fact relying on disruptive colouration rather than background matching as a means of minimizing predation risk was not tested in the present study and needs further investigation. Quantifying the distinct colour patterns of each morph and determining their roles in avoiding visually oriented predators would, therefore, be an integral component of future work.

Negative frequency-dependent selection may also be operating where the rarer plain-backed morphs is less likely to be consumed by predators than the more common patterned morph. Thus, the potentially lowered fitness of being less cryptic could be compensated by being less frequent, thereby providing a selective advantage (Galeotti *et al*. 2003). Although we have not evaluated the effects of frequency-dependent selection, similar survivorship advantages towards predators have been shown in other systems (Bond & Kamil 1998; Fitzpatrick, Shook, & Izally 2009; Olender et al. 2016) and is indicated by the lower frequency of the plain-backed morph in populations where it is sympatric with the patterned morph across the latitudinal cline. To determine whether divergent predator selection is indeed serving to maintain polymorphism in *L. whitii* would require empirical evidence from selective predation experiments.

However, the negative effects of conspicuousness on survivorship of plain-backed morphs may not be resolved solely from cryptic colouration, if at all. Selection on other components of fitness may also favour rare colour patterns (Olendorf *et al*. 2006), including differential reproduction. Divergent levels of fecundity is suggested in *L. whitii* by the variation in interlimb length between morphs and sexes. Females were found to have longer trunks than males, with plain-backed morphs being the longest. Sexual dimorphism in inter-limb length is common among lizards (Forsman & Shine 1995b; Schwarzkopf 2005; Dubey, Chevalley & Shine 2011). It has been suggested that greater abdominal volume is an adaptation towards carrying a greater number of developing offspring (Olsson *et al.* 2002). In having longer interlimb length, plain-backed females should, therefore, have a reproductive advantage over patterned morphs by having larger clutch sizes and ultimately higher overall fecundity throughout their reproductive life. This notion is supported by the fact that plain-backed females in a higher latitude population have been found to have significantly larger litters than patterned females (Chapple 2005). Thus, the reproductive advantage gained by morphological variation may be the single factor enabling the plain-backed morph to increase their survivorship or it may contribute to the anti-predatory strategies of other forms of crypsis aside from background matching, such as disruptive colouration, and/or negative dependent selection.

Drivers of latitudinal morph frequency

Liopholis whitii exhibits opposing patterns of morph frequency where plain-backed morphs generally decrease with latitude while patterned morphs increase. Latitudinal variation in climatic conditions and predation were predicted to be the primary drivers of colour polymorphism in this species. We found that the best predictor of morph frequency was

inferred avian predation pressure while climate was the least influential. Based on the occurrence and dietary information compiled from the literature, the intensity of predation by avian predators was strongest in low latitudes and decreased towards the higher latitudes. Thus, it would be expected then that the least conspicuous morph (patterned) would occur at the highest frequency where the level of avian predation was greatest while the opposite would be true of the most conspicuous morph (plain-backed). Paradoxically, the relationship between *L. whitii* morph frequency and predation intensity does not correspond to the variation in background matching between the morphs. Instead, the incidence of plain-backed morph which has the greatest contrast from their background is highest in low latitudes and lowest in high latitudes, mirroring the pattern of predation intensity. This implies that either background matching among the two colour morphs could vary between populations due to variability in habitat structure or predator communities resulting in different levels of crypsis. Or, other selective forces (i.e., frequency-dependent selection), behavioural differences (i.e., differential dispersal abilities: Forsman *et al*. 2008; Grant & Liebgold 2017), variation in physiology (i.e., thermal tolerances: Bozinovic *et al*. 2011), or non-adaptive processes (i.e., gene flow) not considered here may be occurring across populations and act in producing the observed latitudinal variation in morph frequency in this species. These additional factors should, therefore, be evaluated across populations to help elucidate the underpinnings of colour polymorphism within *L. whitii*.

CONCLUSION

We investigated the functional differences among colour morphs in *L. whitii* using a multi-scale approach. This is the first study that we are aware of that has considered both climate and predation simultaneously as means of evaluating potential trade-offs. Our findings counter much of the previous research on reptiles which demonstrate climate as being most

important and instead we suggest that predation, in terms of either differential levels of crypsis or frequency-dependent selection, may play a primary role in generating ratio-clines in morph frequency. Together, these results provide key insights into the evolution of local adaptation as well as the ecological forces that help explain the dynamics of colour polymorphism. Because colour polymorphism is a complex phenomenon, future studies involving additional populations and more detailed analyses on predation intensity, alternative anti-predatory strategies, such as disruptive colouration, physiology, and behaviour are necessary to gain a more comprehensive understanding of the mechanisms underlying colour polymorphism in this species.

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Author Contributions

Funding for the project was obtained by DGC, GMW and MGG. The project was designed by GM, DGC and CTG. Field work was conducted by GM and ZSA. Analyses was performed by GM, CTG, and KD. The manuscript was written by CTG, KD, and GM, with input from all authors.

Data Accessibility

All data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.b701bs0 (Matthews et al. 2018).

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TABLES

Table 1. Summary of morphological trait variation between sexes and morphs of captured *L. whitii*. All measurements are in mm.

Trait	Patterned Morph				Plain-backed Morph			
	Mean ± SE		*Range*		*Mean ± SE*		*Range*	
	Male	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*	*Female*
SVL	92.7 ± 1.67	90.3 ± 2.56	81.0-108.3	78.7-104.4	94.2 ± 1.55	98.0 ± 1.71	80.6-102.8	89.9-108.6
Mass	22.1 ± 1.50	22.1 ± 2.07	12.1-38.40	13.5-35.3	25.0 ± 1.58	26.9 ± 1.78	12.8-35.3	17.9-38.4
TL	156.1 ± 4.66	148.7 ± 8.42	138.8-164.5	132.5-168.2	169.8 ± 3.50	158.6 ± 8.04	161.6-179.2	144.6-172.5
HW	14.5 ± 0.47	13.7 ± 0.46	12.1-16.3	11.5-15.6	15.5 ± 0.45	14.6 ± 0.43	11.4-18.3	12.5-16.3
HL	23.5 ± 0.33	22.3 ± 0.62	21.4-25.6	20.0-26.3	23.7 ± 0.35	23.4± 0.34	21.5-27.0	22.3-25.6
FLL	18.3 ± 0.28	17.5 ± 18.27	16.0-19.7	13.4-20.5	18.7 ± 0.29	18.9 ± 0.26	16.4-20.4	17.0-19.7
HLL	21.6 ± 0.38	20.5 ± 0.64	19.7-24.1	17.4-22.7	22.4 ± 0.32	21.9 ± 0.33	20.2-24.6	21.4-24.1
ILL	49.5 ± 1.25	47.5 ± 1.86	41.4-62.1	40.8-58.5	49.1 ± 0.94	55.4 ± 1.38	42.6-55.1	49.3-62.1
BW	18.9 ± 0.52	19.5 ± 0.98	15.7-26.7	14.5-24.7	20.4 ± 0.75	22.0 ± 0.73	14.7-26.3	19.1-26.7

Table 2. Results of the general linear models used to evaluate the effects of morph, sex, and their interactions on morphological traits in *L. whitii*. Significant values (< 0.05) are in bold.

Parameter	Fixed Factor	F_{df}	*P*
SVL	Morph	$2.75_{1,45}$	0.11
	Sex	$1.64_{1,45}$	0.21
	Morph x Sex	$0.67_{1,45}$	0.42
Mass	Morph	$0.66_{1,45}$	0.80
	Sex	$0.02_{1,45}$	0.90
	Morph x Sex	$1.06_{1,45}$	0.31
Head Length	Morph	$0.03_{1,45}$	0.87
	Sex	$5.78_{1,45}$	**0.02**
	Morph x Sex	$0.03_{1,45}$	0.87
Head Width	Morph	$1.37_{1,45}$	0.25
	Sex	$3.28_{1,45}$	0.08
	Morph x Sex	$0.24_{1,45}$	0.63
Front Leg Length	Morph	$0.38_{1,45}$	0.54
	Sex	$0.28_{1,45}$	0.60
	Morph x Sex	$0.20_{1,45}$	0.66
Hind Leg Length	Morph	$2.19_{1,45}$	0.15
	Sex	$3.52_{1,45}$	0.07
	Morph x Sex	$0.03_{1,45}$	0.86
Interlimb Lentgth	Morph	$1.88_{1,45}$	0.18
	Sex	$3.49_{1,45}$	0.07
	Morph x Sex	$7.59_{1,45}$	**0.01**
Body Width	Morph	$1.18_{1,45}$	0.28
	Sex	$1.93_{1,45}$	0.17
	Morph x Sex	$0.37_{1,45}$	0.55
Tail Length	Morph	$0.57_{1,14}$	0.47
	Sex	$1.71_{1,14}$	0.22
	Morph x Sex	$4.88_{1,14}$	0.05

Table 3. Effects of morph, sex, and their interactions on the thermal biology and reflectance in *L. whitii* . Field body temperature represents the cloacal body temperature measured upon capture while selected environmental temperature represents the surface temperature measured at lizard capture locations. Significant values (< 0.05) are in bold.

Parameter	**Fixed Factor**	F_{df}	***P***
Thermoregulatory Behaviour	Morph	$0.70_{1,63}$	0.4
	Sex	$2.51_{1,63}$	0.11
	Morph x Sex	$0.74_{1,63}$	0.39
Field Body Temperature	Morph	$0.00_{1,58}$	0.99
	Sex	$2.14_{1,58}$	0.15
	Morph x Sex	$0.65_{1,58}$	0.42
Selected Environmental Temperature	Morph	$0.65_{1,60}$	0.42
	Sex	$3.45_{1,60}$	0.07
	Morph x Sex	$0.01_{1,60}$	0.93
Heating Rate	Morph	$0.19_{1,27}$	0.67
	Sex	$0.17_{1,27}$	0.90
	Morph x Sex	$0.16_{1,27}$	0.70
Parameter	**Fixed Factor**	χ^2	***P***
Average Dorsal Reflectance	Morph	0.48_{1}	0.49
	Sex	1.76_{1}	0.19
	Morph x Sex	0.90_{1}	0.34
Average Right Lateral Reflectance	Morph	0.001_{1}	0.97
	Sex	5.02_{1}	**0.03**
	Morph x Sex	0.49_{1}	0.48
Average Left Lateral Reflectance	Morph	0.22_{1}	0.64
	Sex	0.96_{1}	0.33
	Morph x Sex	0.21_{1}	0.65

Table 4. Results of the GLMs used to evaluate the effect of morph, age, and sex on microhabitat selection of *L. whitii individuals* within 50 cm^2 quadrats sampled at each lizard location. Significant values (< 0.05) are in bold.

Parameter	Estimate (±SE)	*df*	χ^2	*P*
Microhabitat Type				
Morph	0.09 (±0.13)	1	1.34	0.25
Sex	0.18 (±0.12)	1	0.05	0.82
Morph x Sex	-0.40 (±0.20)	1	3.93	**0.05**
% Vegetation Cover < 1 m				
Morph	-0.98 (±0.49)	1	1.59	0.21
Sex	-1.76 (±0.69)	1	0.22	0.64
Morph x Sex	3.10 (±0.93)	1	11.18	**<0.001**
% Vegetation Cover 1-2 m				
Morph	-0.03 (±0.03)	1	0.03	0.87
Sex	-0.03 (±0.02)	1	0.03	0.87
Morph x Sex	0.06 (±0.02)	1	5.92	**0.02**
% Vegetation Cover > 2 m				
Morph	0.14 (±0.67)	1	0.67	0.41
Sex	-0.04 (±0.72)	1	1.23	0.27
Morph x Sex	-1.19 (±1.11)	1	1.15	0.28

Table 5. Effects of morph, sex, and their interactions on the the chromatic and achromatic contrasts between lizard reflectance and habitat reflectance within the quadrats of lizard capture locations. Cone sensitivity and illuminant refer to parameters used in the visual model which explain the different avian visual systems and light conditions under which lizards were captured. Achromatic contrast results are presented only for U-type as there is no known difference in achromatic sensitivities between U-type and V-type visual systems. Upper and lower dorsal contrasts represent the two positions that reflectance was measured on each lizard's dorsal surface. Significant effects are in

				Chromatic Contrast		Achromatic Contrast	
Cone Sensitivity Function	**Illuminant**	**Parameter**	**Fixed Factor**	F_{df}	***P***	χ^2_{df}	***P***
V-Type	Standard Daylight	Upper Dorsal	Morph	$5.40_{1,64}$	**0.02**	–	–
			Sex	$0.003_{1,64}$	0.96	–	–
			Morph x Sex	$0.08_{1,64}$	0.78	–	–
		Lower Dorsal	Morph	$4.66_{1,64}$	**0.04**	–	–
			Sex	$1.93_{1,64}$	0.17	–	–
			Morph x Sex	$0.47_{1,64}$	0.49	–	–
		Average	Morph	$6.34_{1,64}$	**0.01**	–	–
			Sex	$0.52_{1,64}$	0.48	–	–
			Morph x Sex	$0.27_{1,64}$	0.61	–	–
V-Type	Woodland Shade	Upper Dorsal	Morph	$4.71_{1,64}$	**0.03**	–	–
			Sex	$0.001_{1,64}$	0.98	–	–
			Morph x Sex	$0.16_{1,64}$	0.69	–	–
		Lower Dorsal	Morph	$3.60_{1,64}$	0.06	–	–
			Sex	$1.73_{1,64}$	0.19	–	–
			Morph x Sex	$0.57_{1,64}$	0.45	–	–
		Average	Morph	$5.24_{1,64}$	**0.03**	–	–
			Sex	$0.46_{1,64}$	0.50	–	–
			Morph x Sex	$0.39_{1,64}$	0.54	–	–
U-Type	Standard Daylight	Upper Dorsal	Morph	$1.43_{1,64}$	0.24	3.97_1	0.05
			Sex	$0.05_{1,64}$	0.82	2.28_1	0.13
			Morph x Sex	$0.91_{1,64}$	0.34	3.97_1	0.05
		Lower Dorsal	Morph	$0.37_{1,64}$	0.55	0.02_1	0.89
			Sex	$0.77_{1,64}$	0.38	1.61_1	0.20
			Morph x Sex	$1.08_{1,64}$	0.30	0.42_1	0.52
		Average	Morph	$1.01_{1,64}$	0.32	0.99_1	0.32
			Sex	$0.12_{1,64}$	0.73	1.49_1	0.22
			Morph x Sex	$1.20_{1,64}$	0.28	1.51_1	0.22
U-Type	Woodland Shade	Upper Dorsal	Morph	$0.74_{1,64}$	0.39	4.86_1	**0.04**
			Sex	$0.07_{1,64}$	0.80	2.52_1	0.11
			Morph x Sex	$1.26_{1,64}$	0.27	4.27_1	**0.04**
		Lower Dorsal	Morph	$0.05_{1,64}$	0.83	0.04_1	0.84
			Sex	$0.63_{1,64}$	0.43	1.73_1	0.19
			Morph x Sex	$1.40_{1,64}$	0.24	0.50_1	0.48
		Average	Morph	$0.36_{1,64}$	0.55	1.08_1	0.30
			Sex	$0.08_{1,64}$	0.78	1.58_1	0.21
			Morph x Sex	$1.61_{1,64}$	0.21	1.60_1	0.21

Table 6. Model comparison for morph frequency across latitude. Climate is derived from the combined effect of average annual rainfall and average annual maximum and minimum temperature. dAIC represents the delta corrected Akaike information criterion. The lowest dAIC indicates the best model which is presented in bold.

Model	Predictors					*df*	AIC Weight	dAIC
3		Bird			# pattern morph	2	0.7	**0.0**
8	Climate	Bird	Reptile	Mammal	# pattern morph	7	0.2	2.3
1	Climate	Bird			# pattern morph	5	0.1	3.5
4	Climate		Reptile		# pattern morph	5	8.8×10^{5}	18.0
5	Climate			Mammal	# pattern morph	5	2.1×10^{5}	20.7
7			Reptile		# pattern morph	2	1.1×10^{8}	35.9
6				Mammal	# pattern morph	2	7.6×10^{10}	41.2
2	Climate				# pattern morph	4	4.6×10^{27}	120.5

FIGURES

Figure 1. Geographic distribution of the patterned (a) and plain-backed (b) *L. whitii* colour morphs. Percentages represent the relative incidence of each morph per latitudinal band. Total *n* = 2045 including the patternless morph (not shown). Maps, photos and frequencies are taken from Chapple et al. (2008).

Figure 2. Comparison of microhabitat type used by each *L.whitii* morph by sex.

Figure 3. Comparison of chromatic and achromatic contrasts between *L. whitii* morphs and microhabitats. Contrasts are presented for both V-type and U-type visual systems and both illuminants used in the visual modelling. Achromatic contrast results are presented only for U-type as there is no known difference in achromatic sensitivities between U- and V-type visual systems. Just noticeable differences (JND) greater than one are indicative of low levels of background matching and thus increased conspicuousness to avian predators.

Figure 4. Frequency of *L. whitii* morph occurrence across this species' latitudinal distribution as a function of avian predation intensity. Solid and dotted black lines represent the percentage of each morph within each latitudinal band. Red line depicts percentage of total predation score within each band.